

DEDUCING THE BODY POSTURE OF EXTINCT LARGE VERTEBRATES FROM THE SHAPE OF THE VERTEBRAL COLUMN

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ABSTRACT. Simple measurements were taken from the vertebral column of several extinct and extant terrestrial vertebrates in order to estimate the bending moments in a sagittal plane that could be sustained along the longitudinal body axis. According to theoretical expectations, the estimated patterns of sustainable bending moments prove to differ between bipeds and quadrupeds of different body proportions. In an analysis of the vertebral column of the dinosaurs *Plateosaurus* and *Iguanodon*, the former appears as a habitual quadruped, while the latter must have assumed a bipedal posture more frequently or carried most weight on the hindlimbs during quadrupedal locomotion. A separate analysis of the cross sectional areas of the vertebral centra and the lever arms of the epaxial muscles gives further information on the use of the vertebral column during locomotion and reveals aspects of the ecology of the animals under study.

EVEN if complete skeletons of an extinct species are preserved, the possible arrangements of the fossilized bones usually leave open some questions about body and limb posture. Slight changes of the relative positions of adjacent bones may summate over several joints in the limbs or in the vertebral column, so that quite different reconstructions of the same animal can be obtained. A prosauropod dinosaur, for example, may be reconstructed bipedally or quadrupedally, its limbs may appear rather sprawling or column-like and the neck might be placed nearly horizontally or more vertically (Galton 1976; van Heerden 1979; Cooper 1981; Weishampel and Westphal 1986; Christian *et al.* in press). There might be other clues like hooves on the finger tips indicating a quadrupedal body posture in some fossil vertebrates or there may be fossilized tracks that can be attributed to a particular genus with a high probability. Such fossilized tracks are not only helpful in deciding whether the track-maker was moving bipedally or quadrupedally but also in estimating the centre of mass and the gait of the animal (e.g. Alexander 1989; Thulborn 1990). However, even if such evidence is available, postures and gaits that do not fit the tracks usually cannot be excluded. A track-maker, for example, that only left tracks demonstrating quadrupedal locomotion, may have used a bipedal gait as well in situations that are not documented.

Different body and limb postures are not only associated with different arrangements of the bones, they also evoke different patterns of stresses in the skeleton (e.g. Kummer 1959; Pauwels 1965; Preuschoft 1969, 1970, 1971, 1976). If the skeletal remains of an extinct vertebrate are analysed with regard to the forces and torques that could be sustained, we can obtain further important evidence on the possible postures and gaits of this animal (Preuschoft 1976; Alexander 1985; Christian *et al.* in press).

In this study we investigate how the predominant body posture of a dinosaur (or any other terrestrial vertebrate) can be derived from the shape of the vertebral column even if the distribution of body mass is not reliably known. Based on a method similar to that developed by Preuschoft (1976) to deduce the patterns of bending moments and compressive forces in the vertebral column along the body axis, we compare the shapes of the vertebrae of several extinct and extant vertebrates that can be classified clearly as either exclusively bipedal or exclusively quadrupedal. The method is then applied to the prosauropod *Plateosaurus* and the ornithopod *Iguanodon*, the body postures of which are still the subject of controversy.

MATERIAL

Measurements were taken from vertebrae of five extant vertebrates (two mammals, two birds and one reptile) and seven dinosaurs, as listed below.

Bipeds. *Macropus giganteus* (Grey Kangaroo), SMF 53503: Senckenberg-Museum, Frankfurt, Germany (this species is included here because it is quadrupedal only at very low speeds of locomotion); *Rhea americana* (Rhea), SMF 2398: Senckenberg-Museum, Frankfurt, Germany; *Struthio camelus* (Ostrich), Institute d' Anatomie, Strasbourg, France; *Albertosaurus* (theropod dinosaur), Royal Tyrrell Museum, Canada, cast of ROM 1247, the original skeleton in the Royal Ontario Museum, Toronto, Canada; *Tarbosaurus* (theropod dinosaur), exhibition from Mongolia, touring through Germany in 1994; *Tyrannosaurus* (theropod dinosaur), exhibited cast in the Senckenberg-Museum, Frankfurt, Germany.

Quadrupeds. *Varanus salvator* (monitor lizard), ZFMK 5137A, Koenig Museum, Bonn, Germany; *Capra ibex* (Ibex), SMF 1461, Senckenberg-Museum, Frankfurt, Germany; *Dicraeosaurus* (sauropod dinosaur), exhibited specimen in the Museum für Naturkunde, Humboldt University, Berlin, Germany; *Chasmosaurus* (ceratopsian dinosaur), Royal Tyrrell Museum, Canada, from a copy of ROM 5499, the original skeleton in the Royal Ontario Museum, Toronto, Canada.

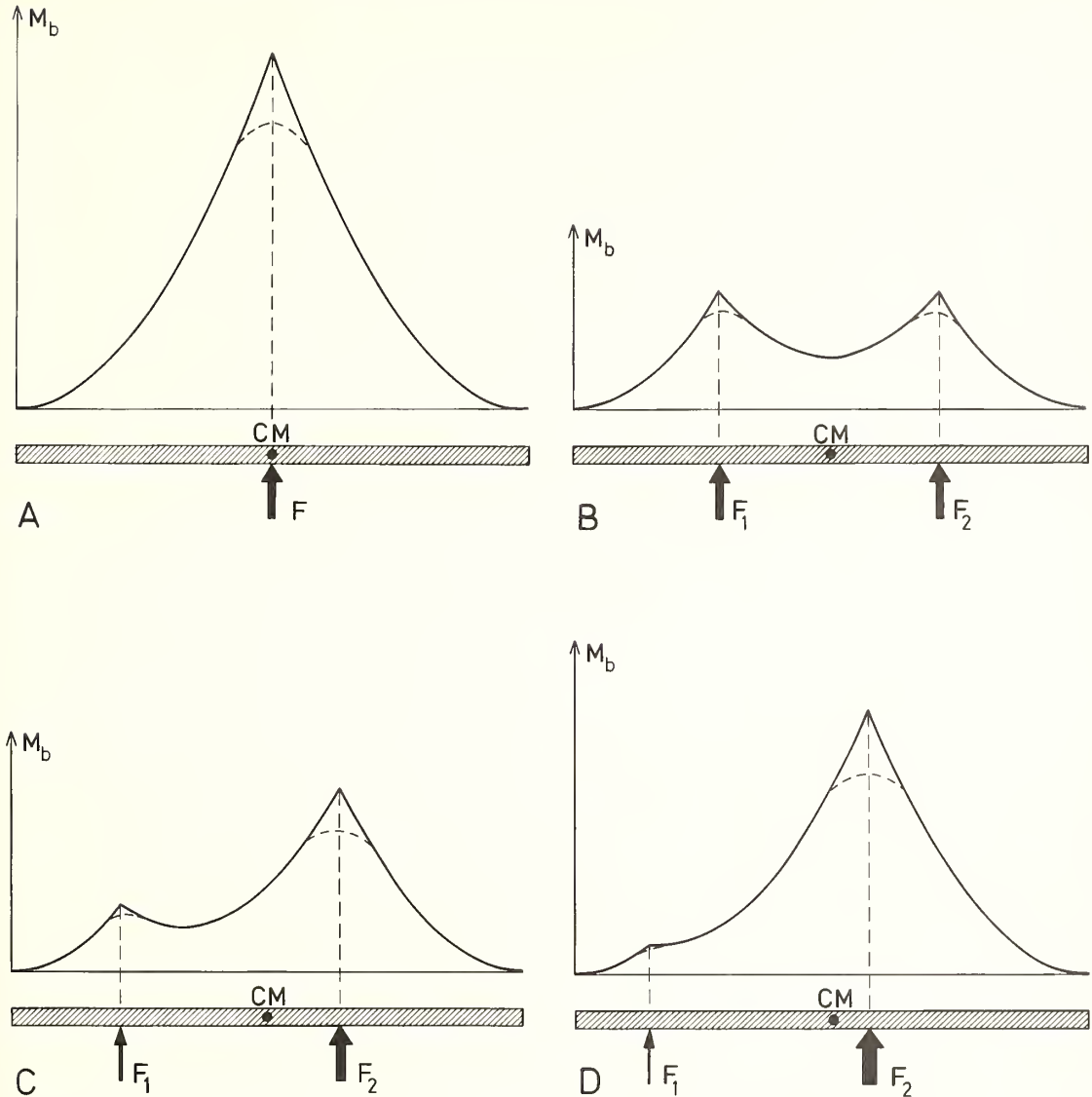
Others. *Plateosaurus* (prosauropod dinosaur), reg.-no. 1668/1, Universität Tübingen, Germany; *Iguanodon bernissartensis* (ornithopod dinosaur), exhibited cast in The Natural History Museum, London.

BENDING MOMENTS, POSTURE AND MASS DISTRIBUTION

Depending on posture and distribution of body mass, the neck, trunk and tail of a resting animal experience forces and torques (bending moments). Bending moments along the longitudinal body axis act primarily in a sagittal plane unless parts of the body, e.g. the tail, are accelerated quickly sideways.

The pattern of bending moments along the vertebral column is distinctively different between quadrupedal and bipedal animals as demonstrated schematically in Text-figure 1. In side view, a bipedal animal can be simplified as a beam carried by one pillar, a quadrupedal animal as a beam carried by two pillars. The bending moments M_b can then be calculated according to the rules of statics (e.g. Pauwels 1965). In a biped (Text-fig. 1A), the bending moments will be maximal at the hips and drop towards both the cranial and the caudal end of the body. The bending moments are considerably higher at the middle of the trunk (midpoint between hips and shoulders) than they are at the shoulders. In a quadruped (Text-fig. 1B-D), on the other hand, there will be two peaks in the curve of bending moments along the vertebral column, one at the hips and one at the shoulders. Between shoulders and hips, the bending moments will decrease and, depending on the distribution of body mass, may reach an opposite direction approximately at the middle of the trunk, thereby changing from hogging moments, which tend to bend the body convex at the dorsal surface, to sagging moments, which tend to bend the body concave at the dorsal surface. The point of minimal hogging (or maximal sagging) moments can be located close to one pair of limbs if the other pair of limbs carries most of the body weight (Text-fig. 1C-D). With an extremely small share of body weight carried by one pair of limbs, or if shoulders and hips are located close together compared to total body length, there might be only a slight drop or even no drop at all in the hogging moments between shoulders and hips (Text-fig. 1D), so that the pattern of bending moments resembles that of a biped.

If the feet are not placed below the shoulder or hip joints, respectively, vertical ground reaction forces will induce torques about these joints. Then muscles at these joints have to become active



TEXT-FIG. 1. Bending moments M_b in the sagittal plane along a homogeneous beam with a constant cross section. In A the beam is carried by one support; in B-D the beam is carried by two supports. The weight is carried equally by both supports in B and shifted towards the right from B to D. F , F_1 and F_2 are the reaction forces that are exerted by the supports on the beam.

which pulls the trunk up- or downwards, thereby increasing the bending moments between the proximal joint of the extremity and the area where the muscle force is transmitted to the trunk. Such muscle activities, however, will not change the general differences in the patterns of bending moments between quadrupeds and bipeds as described above. The well-developed pelvic girdle and, if present, a well-developed pectoral girdle, sternum and ribs distribute the forces transmitted by the limbs over a certain area and may take over some of the bending moments, so that the peaks in the curve of bending moments will be blunted (Preuschoft 1976; Alexander 1985; Preuschoft and Günther 1994). The reduction of the bending moments at hips and shoulders is indicated by the

broken lines in Text-figure 1, which are more realistic than the unbroken lines for the bending moments along the trunk axis of dinosaurs and many other vertebrates.

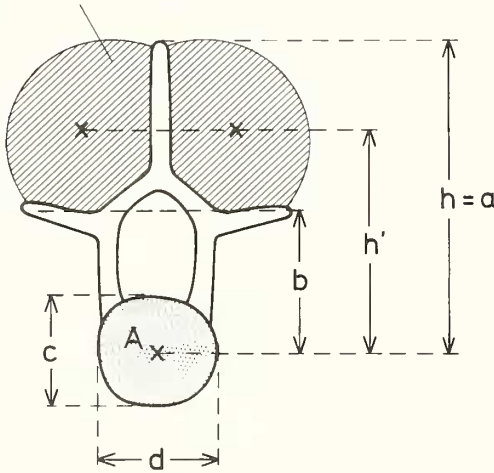
The highest forces and moments acting on an animal do not occur during rest but in fast locomotion (e.g. Alexander 1982, p. 81; Preuschoft 1989; Christian 1995). During fast locomotion, we have to take into account forces due to inertia and the fact that not all feet are placed on the ground simultaneously. Besides, the position of the feet relative to the proximal joints of the extremities change during a stride, as well as the direction and the magnitude of the ground reaction forces, and to a lesser degree also the shape and spatial orientation of the trunk (e.g. Preuschoft and Fritz 1977; Preuschoft and Günther 1994). If, however, the highest bending moments that occur during a complete cycle are calculated for each position along the trunk, we will still get a pattern that does not deviate essentially from what has been found at rest (see Preuschoft and Fritz (1977) for a detailed analysis of the bending moments along the trunk axis of a horse during locomotion). It should be mentioned that our analysis cannot be applied without further examination on animals that do not experience the highest forces and torques during terrestrial locomotion on firm ground.

VERTEBRAL SHAPE AND THE PATTERN OF BENDING MOMENTS

Sagging bending moments, which may occur in the middle of the trunk of some quadrupedal vertebrates (see above), can be counteracted by tension in abdominal muscles and compressive forces in the vertebral column. More important for our analysis are hogging bending moments.

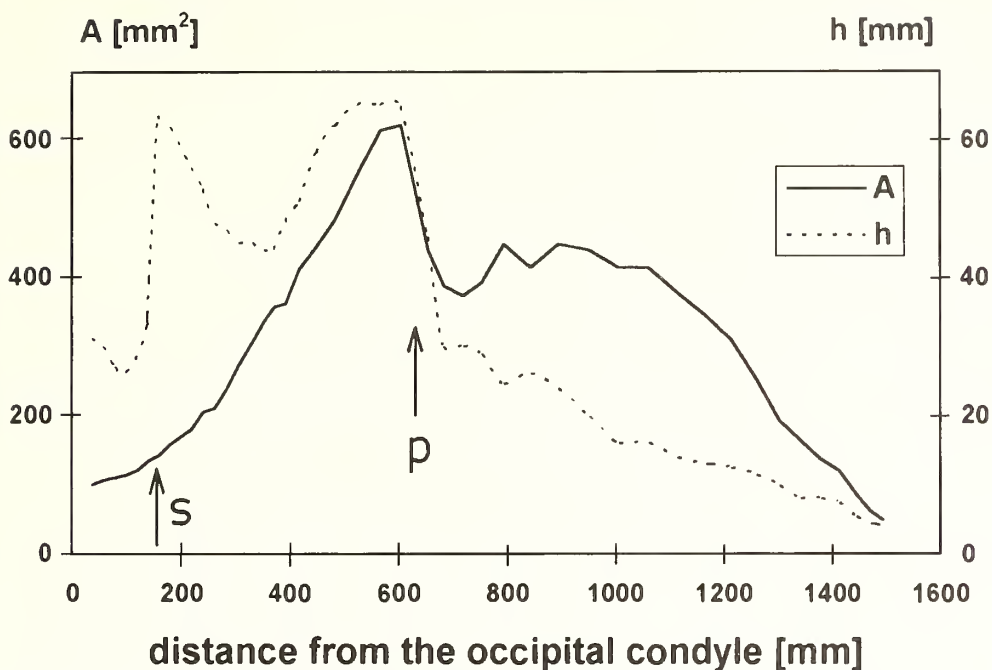
Hogging bending moments must be counteracted at the intervertebral junctions by tension in epaxial muscles which are supported by ligaments that connect the spinal processes (Text-fig. 2; see

epaxial muscles



TEXT-FIG. 2. Schematic caudal view of a vertebra. The measurements a, b, c and d were taken to calculate the lever arm of the epaxial muscles and the cross sectional area A of the vertebral centrum, as explained in the text. h: lever arm estimated according to Alexander (1985), h': lever arm estimated according to Preuschoft (1976).

also Preuschoft 1976; Alexander 1985, 1989). A muscle force F acting in a sagittal plane at a distance h above the transverse axis of an intervertebral joint produces a torque $F \times h$ about that joint; h is the lever arm of the force F . The lever arm is the distance between the line of action of the force and the axis of the joint. The torque can be increased by either increasing the force, the lever arm, or both. The transverse axis of an intervertebral joint can be assumed to pass through the centre of the intervertebral disc (Preuschoft 1976; Alexander 1985). The lever arms of the epaxial muscles can be estimated from the shape of the vertebrae. Preuschoft (1976) assumed h to be equal to the vertical distance between the centre of the epaxial muscles and the centre of the intervertebral discs. He suggested that h be estimated to be equal to $(a+b)/2$ with a the distance from the midpoint of the vertebral centrum (vertebral body) to the tip of the spinal process and b the distance

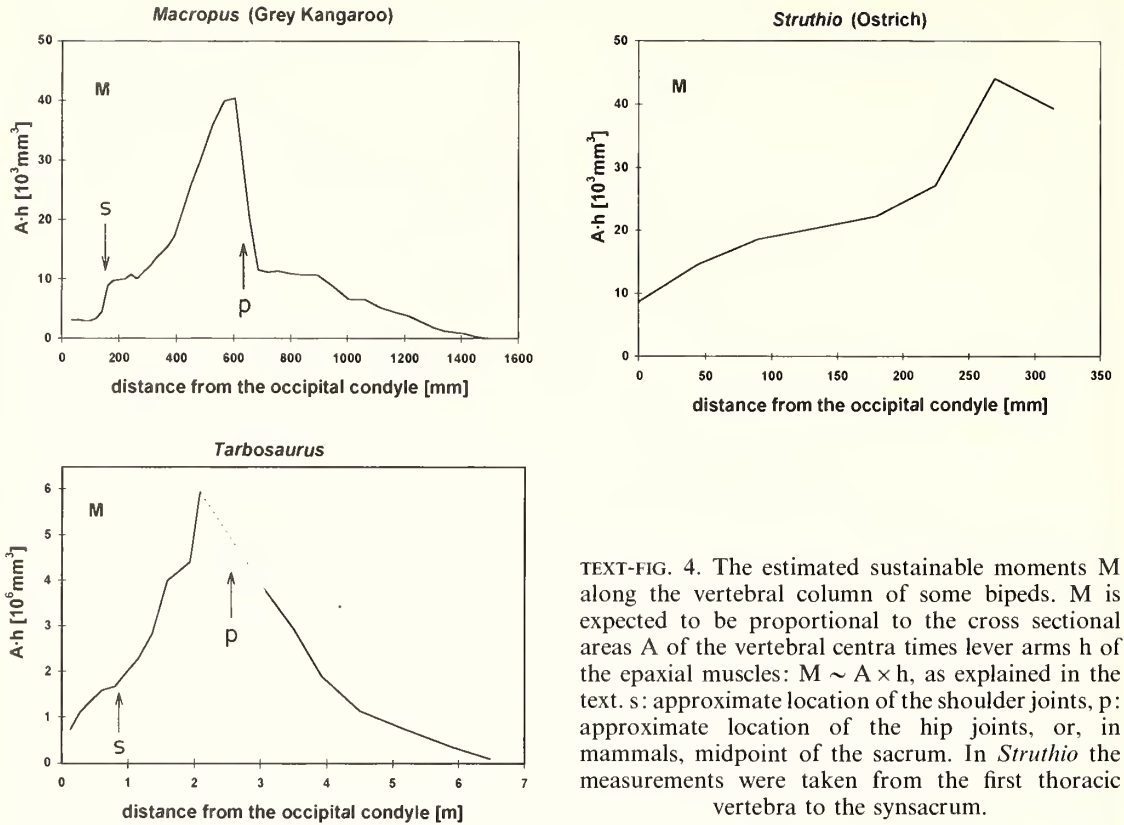


TEXT-FIG. 3. Lever arms h of the epaxial muscles and cross sectional areas A of the vertebral centra along the vertebral column of *Macropus giganteus* (Grey Kangaroo). s : approximate location of the shoulder joints, p : pelvis, midpoint of the sacrum.

from the midpoint of the vertebral centrum to the bases of the transverse processes (see Text-fig. 2). For some dinosaurs, Alexander (1985) found it more likely that the muscle force F was transmitted mainly by tendons close to the tips of the spinal processes. He estimated h to be equal to a . For our purpose, both methods lead to similar results (see below). Further problems in estimating h arise if epaxial muscles or their tendons are located far above the spinal processes. This is unlikely in the trunk but quite common in the necks of mammals (e.g. Preuschoft and Fritz 1977; Preuschoft and Günther 1994).

The maximum muscle force F at a given position in the vertebral column seems to be difficult to obtain, because the functional cross section of the epaxial muscles cannot be deduced from skeletal remains. Preuschoft (1976), however, pointed out, that the pulling force F of the epaxial muscles evokes a compressive force of the same magnitude between the vertebral centra. Therefore, under the assumption of equal safety-factors along the vertebral column, the highest regularly occurring forces F should be proportional to the transversal cross sections of the centra or of the intervertebral discs. The cross sections A of the intervertebral discs may be the better measure for the compressive forces and can be assumed to be approximately equal to the surface areas of the adjacent vertebral centra (Preuschoft 1976). It has been argued that bending moments could also be counteracted by elevated pressure in the body cavity (Preuschoft *et al.* 1979; Alexander and Jayes 1981). Alexander (1985), however, stated that for dinosaurs such elevated pressure could not be maintained while breathing in. Anyway, if elevated pressure in the body cavity takes over a fraction of the compressive forces, this fraction will be similar between shoulder and hip joint and therefore not affect much the general pattern of compressive forces acting along the vertebral column of the trunk.

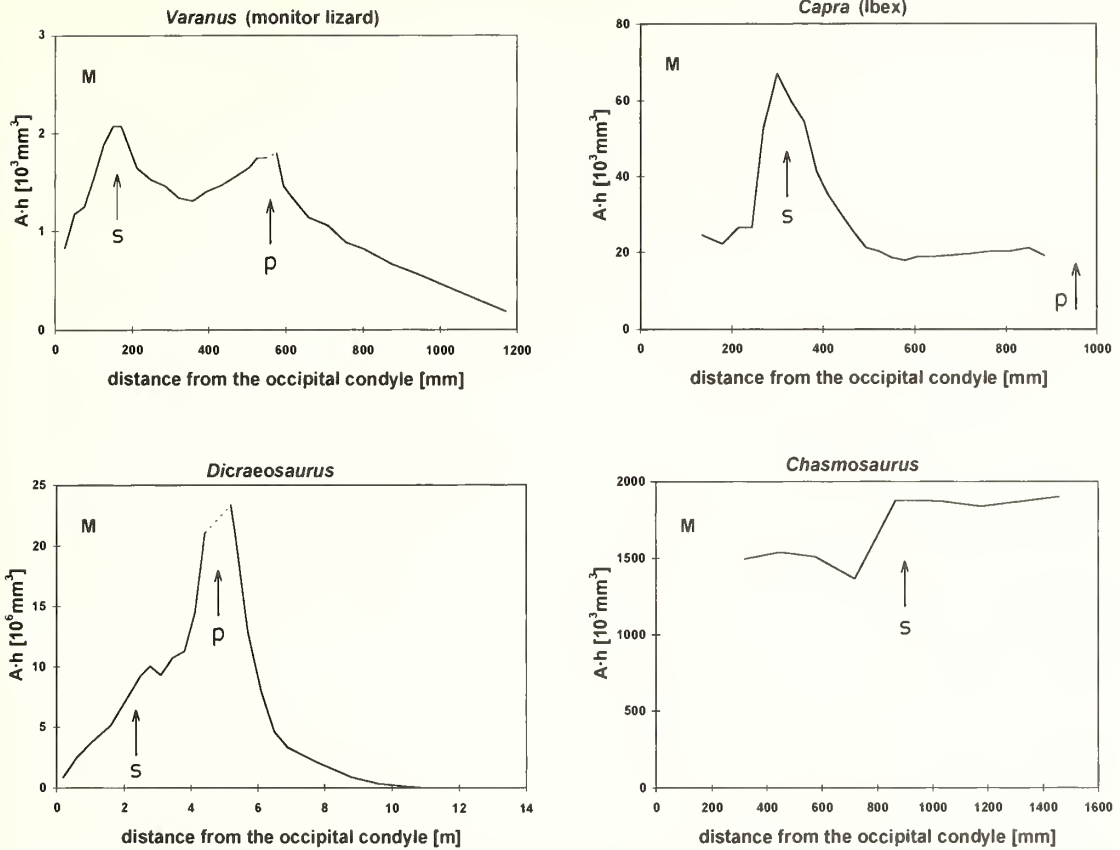
To calculate A and h , the length measurements a , b , c and d , as defined in Text-figure 2, were taken with calipers at the caudal end of the vertebrae. The area of the caudal surface of each



TEXT-FIG. 4. The estimated sustainable moments M along the vertebral column of some bipeds. M is expected to be proportional to the cross sectional areas A of the vertebral centra times lever arms h of the epaxial muscles: $M \sim A \times h$, as explained in the text. s : approximate location of the shoulder joints, p : approximate location of the hip joints, or, in mammals, midpoint of the sacrum. In *Struthio* the measurements were taken from the first thoracic vertebra to the synsacrum.

centrum was calculated by assuming an elliptical shape with c and d as major axes. In the thoracic region, compressive forces between adjacent centra can be exchanged partly by the heads of the ribs. If the surface areas of the rib articulations at the caudal end of a vertebra were not negligibly small, they were added to the caudal surface area of the centrum to obtain A . Distances from the occipital condyle were measured with a tape ventrally along the vertebral centra. A was multiplied by h to obtain a measure for the moment M that can be produced by the epaxial muscles at a given location of the vertebral column. M is equivalent to the highest sustainable (hogging) bending moment. The distribution of h and M along the vertebral column differed only slightly between the two methods of estimating the lever arms of the epaxial muscles. Therefore, we present only the data with h estimated to be equal to the distance between the midpoint of the vertebral centrum and the tip of the spinal process.

Because of the reciprocal interdependence of lever arms of muscles and compressive forces in the vertebral column, there are always two possibilities in each animal: the lever arms may correlate either with the pattern of bending moments, or with the cross sectional areas. Both may be true and are mechanically equivalent. The data of Preuschoft (1976) on *Diplodocus* and Alexander (1985) on *Diplodocus* and *Iguanodon* as well as our own data on most of the animals studied here are in accordance with the assumption that the pattern of bending moments is already reflected in the lever arms of the epaxial muscles along the vertebral column. Some data like those on *Macropus* (Text-fig. 3), however, are clearly contradictory, demonstrating that the patterns of h and A can be quite different. We therefore prefer to use the full information of lever arms and cross sectional areas to estimate the sustainable bending moments.



TEXT-FIG. 5. The estimated sustainable moments M along the vertebral column in selected quadrupeds. Explanations as in Text-figure 4.

BIPEDS AND QUADRUPEDS COMPARED

Bipeds. In all bipeds examined in this study, the moment M reaches its maximum at the hips and drops continuously towards both ends of the body with no local maximum or plateau at the shoulders (Text-fig. 4). The general pattern of the estimated moments M is similar in the three theropods so that only the data for *Tarbosaurus* are presented, although M decreases more towards the head in this species, especially if compared with *Albertosaurus*. The data for *Rhea* are not presented either, because they are very similar to those of *Struthio* (as well as additional data for other ratites). In *Macropus*, in the neck and at the base of the tail h is underestimated, because in these areas some tendons and muscles are located far away from the spinal processes of the vertebrae as in the neck of many other mammals, e.g. horses. In fossils, we usually can only guess whether there were ligaments or muscles present above the spinal processes. This, however, is very uncommon in the vertebral column between shoulders and hips of all extant vertebrates and, in view of the usually high spinal processes in this section, is unlikely in most dinosaurs.

Quadrupeds. In Text-figure 5 the patterns of the estimated moments M along the body axis are plotted for all quadrupeds studied here. A recalculation of the data for *Diplodocus* presented by Preuschoft (1976) gives results very similar to those for *Dicraeosaurus*.

In all specimens, the pattern of M is in accordance with our expectations. Around the shoulders, there is always a local maximum or at least a plateau visible. The pattern in the monitor lizard is

similar to that given in Text-figure 1b with two distinct peaks of M of roughly similar size at the shoulders and hips. In the monitor, however, the tail is longer and heavier than head and neck, so that we would expect a higher local maximum at the hips than at the shoulders. Therefore, the pattern of bending moments, if derived from the actual distribution of body mass, is rather similar to the pattern given in Text-figure 1c. The relatively higher moments M that can be sustained at neck and shoulders might be due to activities other than locomotion. The monitor is a predator which sometimes uses strong movements of head and neck while killing prey.

In the sauropods, there is only a slight reduction of M between shoulders and hips below the values found at the pectoral girdle. This is in accordance with our expectation for animals with well-developed pectoral girdles that distribute the loads transmitted through the shoulder joints over a long section of the trunk, and which carry much more weight on the hindlimbs than on the forelimbs, as illustrated in Text-figure 1d (see also Preuschoft (1976) and Alexander (1985) for the statics of *Diplodocus*). The location of the more cranial maximum in the pattern of M behind the shoulders instead of directly at the shoulders leads to the conclusion that either the shoulder joints were located more caudally than in the reconstructions used for our measurements or that the forefeet were placed behind the shoulder joint. Another possible explanation of the data would be to invoke tendons or ligaments far away from the spinal processes in the shoulder region. This latter possibility, however, seems rather improbable in view of the high spinal processes in this region, as mentioned before.

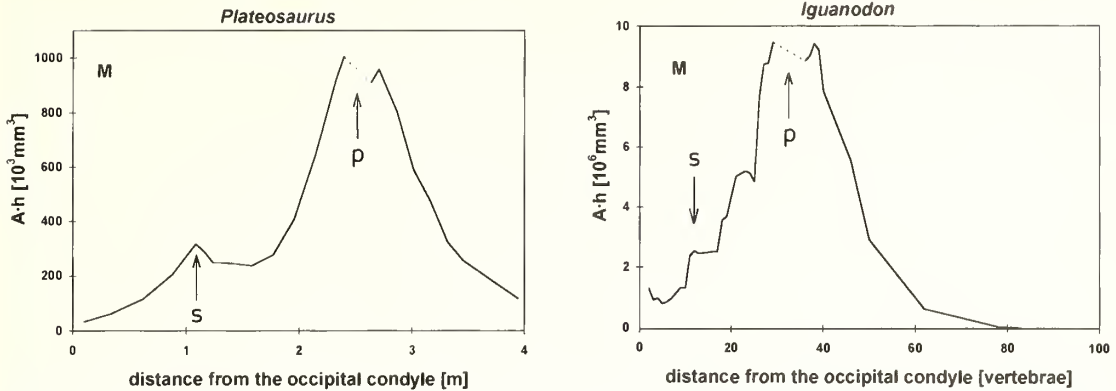
The situation is reversed in *Capra*, which has a long neck and a very short and light tail so that no peak of the moments occurs at the hips, provided the animal stands with the hindlimbs more or less perpendicular.

The data from the vertebral column of *Chasmosaurus* (Text-fig. 5) are problematical for our analysis, because its armour indicates that activities other than locomotion might have been the primary factors for the shaping of the vertebral column (see below). Furthermore, the expanded pectoral girdle may have distributed the forces transmitted by the forelimbs over such a long section that there was no clear maximum of the bending moments close to the shoulders. Nevertheless, the estimated moment M is about constant from the base of the neck to the middle of the trunk in *Chasmosaurus*, in accordance with our expectations for the pattern of bending moments in a quadruped with a well-developed pectoral girdle, and distinctively different from all the examined bipeds in which M decreases continuously from the sacrum towards the shoulders.

Plateosaurus and *Iguanodon*. As mentioned before, the body posture of *Plateosaurus*, as well as of other prosauropods, is not reliably known (Galton 1976; van Heerden 1979; Weishampel and Westphal 1986; Christian *et al.* in press). Individuals in museums are placed sometimes in quadrupedal and sometimes in bipedal postures. It is possible that *Plateosaurus*, like many modern lizards (Christian *et al.* 1994a, 1994b; Christian 1995), became bipedal at high speeds, being otherwise quadrupedal. Some fossil tracks of bipeds have been attributed to prosauropods, but this interpretation has been questioned (see Thulborn 1990, p. 176, for a detailed analysis of fossil prosauropod tracks).

The pattern of M along the vertebral column in *Plateosaurus* shows two distinct local maxima at shoulders and hips (Text-fig. 6). The peak at the hips is much higher than the peak at the shoulders. The moments evidently have been rather low along the whole length of the neck. These observations are consistent with a quadrupedal body posture and a more or less vertical neck posture. A bipedal posture may have been assumed occasionally but the data do not fit a habitually bipedal posture. *Plateosaurus*, therefore, appears to have been a habitual quadruped, which may have used a bipedal gait infrequently at its fastest locomotion, or during standing.

For *Iguanodon*, some evidence from tracks and from the skeleton indicate that this dinosaur used a quadrupedal gait at low speeds and a bipedal gait at high speeds of locomotion (Currie and Sarjeant 1979; Norman 1986; Norman and Weishampel 1990; Thulborn 1990, p. 190). The vertebrae of *Iguanodon* available for this study are in a less well-preserved condition than those of *Plateosaurus*, so that the curve of M is less smooth (Text-fig. 6). The pattern of the moment M ,



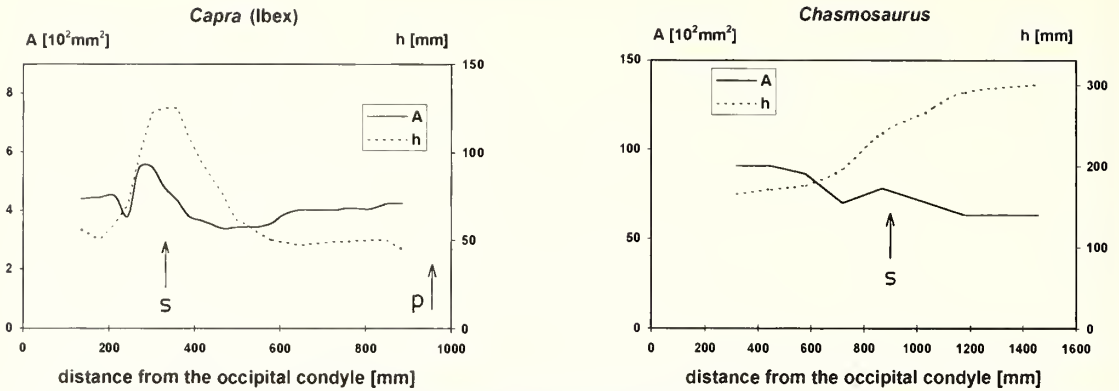
TEXT-FIG. 6. The estimated sustainable moments M along the vertebral column of *Plateosaurus* and *Iguanodon*. Explanations as in Text-figure 4.

however, has only one pronounced peak at the hips. Towards the head M decreases continuously, though there might be a plateau or a much less pronounced second peak at the shoulders. The overall pattern of bending moments along the body axis is very similar to that of *Macropus* (Text-fig. 4), which is also very similar to *Iguanodon* in its overall body proportions. Therefore, the data for *Iguanodon* are in accordance to a frequent use of a bipedal body posture especially during fast locomotion and a quadrupedal posture which was used only at slow speeds as in kangaroos. The plateau or low local maximum of the bending moments at the shoulders might indicate a minor shaping influence of the quadrupedal posture that was probably assumed at low speeds, as in kangaroos. A quadrupedal posture at high speeds of locomotion is only in accordance with the data if very little weight was carried by the forelimbs.

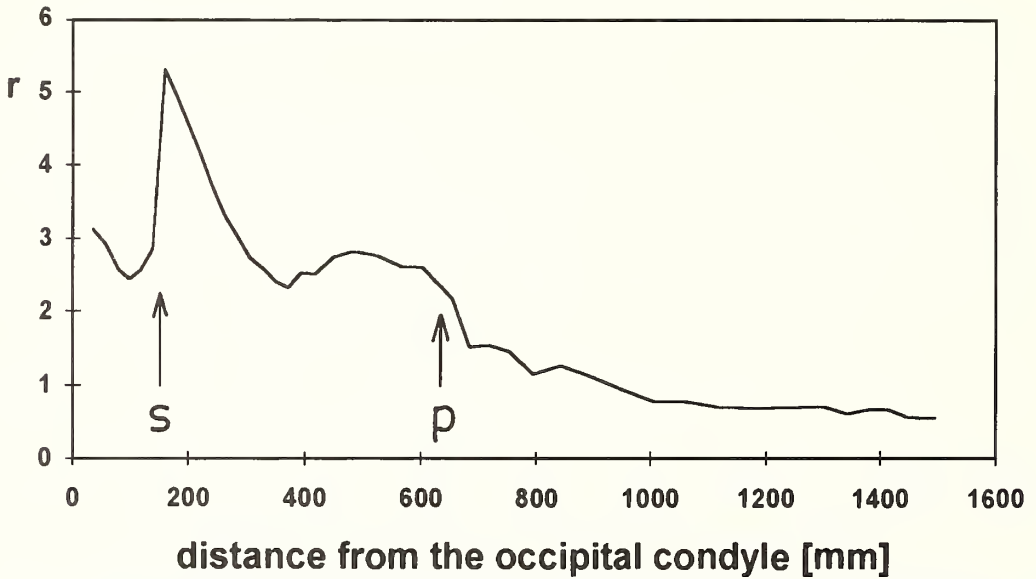
ADDITIONAL INFORMATION ABOUT LIFE-STYLE

For extinct animals, assessments of the distribution of body mass are usually highly speculative. In our approach to determine the body posture from the shape of the vertebral column, we do not need much knowledge about the distribution of body mass of the examined animals. If, on the other hand, a reasonable and reliable model of an animal is available, a reconstruction of the pattern of bending moments along the vertebral axis may allow a reconstruction of the posture of the neck and tail, as well, as demonstrated by Preuschoft (1976) for *Diplodocus* and mentioned above for the neck posture of *Plateosaurus*. The neck and tail of vertebrates, however, are often involved in activities other than locomotion, so that in some animals they might be much stronger than necessary to cope with regular forces and torques during locomotion, as discussed above for *Varanus*. In goats and probably also in ceratopsians like *Chasmosaurus* the heads are utilized in strenuous ritual combat (Farlow and Dodson 1975; Alexander 1989, p. 73; Dodson and Currie 1990). Accordingly, the sustainable moments M are relatively high in the necks of *Capra* and *Chasmosaurus* (Text-figs 4–5). Especially in the distribution of the cross sections A of the vertebral centra in the neck and at the shoulders, a characteristic situation is found in both species (Text-fig. 7). The cross sections A decrease towards the head in all other animals studied here except in these two species in which A is about constant between shoulders and head (*Capra*) or increases slightly towards the head (*Chasmosaurus*). This is to be expected in association with the high compressive forces in the cervical spine during the head-to-head fighting undertaken by goats.

The relatively high estimates for the moments at neck and shoulders in *Albertosaurus* compared with the other theropods studied here, especially *Tarbosaurus*, might result from differences in the distribution of body mass of the theropods examined; alternatively, it might indicate an involvement of trunk and neck in more strenuous activities in *Albertosaurus*, such as the killing of



TEXT-FIG. 7. Lever arms h of the epaxial muscles and cross sectional areas A of the vertebral centra along the vertebral column of *Capra ibex* (Ibex) and *Chasmosaurus*.



TEXT-FIG. 8. The ratio r between the lever arm h of the epaxial muscles and the cross sectional area A of the vertebral centra along the vertebral column of *Macropus giganteus* (Grey Kangaroo).

large prey. For a conclusive analysis, however, reliable estimates of the distribution of body mass in the three species, and data from the vertebral columns of several individuals of each species would be necessary.

As mentioned above, a particular torque can be produced either by a high force and a short lever arm, or by a low force and long lever arm. The first solution permits rapid movements, the second solution is not adequate for rapid movements but permits stabilization of the joint with little force and energy expense. Therefore, comparing h and A , as measures for lever arm and force, respectively, provides additional information on the mechanics of the longitudinal body axis.

In *Macropus*, for example, head and neck are held in a relatively fixed position during locomotion, while tail and lumbar region are very active during hopping. Accordingly, A remains high in the proximal part of the tail, where the vertebral column is compressed by muscles that move the tail, while A drops quickly from the sacrum towards the head (Text-fig. 3). The lever arms are

long at the shoulders, thereby allowing economical stabilization of the neck during locomotion. For a quantitative comparison of lever arms and forces that can also be used across species, we might use the dimensionless ratio r , which is h divided by the square root of A . The ratio r should be high in regions of the vertical column that are not involved in rapid movements in a sagittal plane. The reverse ratio $1/r$ might be used as a measure for 'agility'. In Text-figure 8, r is plotted along the vertebral column of *Macropus*, further illustrating the analysis given above. The ratio r is high in the thorax but much lower everywhere else, especially in the tail, which is not only flexed and extended periodically during locomotion but also used actively to balance the body.

(Semi)bipedal ornithopods usually have long lever arms h of the epaxial muscles especially around the hips (e.g. Norman 1986; Norman and Weishampel 1990) where the highest bending moments occur, so that tail and trunk could be kept straight with little force and low energy expenditure. Similar-sized theropods, on the other hand, tend to have shorter lever arms, but higher cross sectional areas of the vertebral centra, indicating that the vertebral column was involved in forcefully performed rapid movements such as might have occurred during predation. Along the trunk, the average ratio r of the lever arm h divided by the square root of A is about 2.2 for *Tarbosaurus* and *Albertosaurus*, about 2.9 for *Tyrannosaurus* and between 3.0 and 3.5 for *Iguanodon*. At the base of the tail, r is about 2, or slightly higher, in *Tarbosaurus* and around 3 in *Iguanodon*. In the light of these results, *Albertosaurus* appears as a ferocious predator, well suited for killing large as well as agile prey by rapid and forceful attacks with its head.

CONCLUSIONS

We conclude that the shape of the vertebral column reflects body posture. The bending moments which can be resisted by neck, trunk, and tail can be described sufficiently with simple measurements taken from a sufficient number of vertebrae. The pattern of bending moments along the longitudinal body axis is determined by mass distribution and body posture. Because of their relationship, it is possible to predict one variable if the others are known, or are estimated independently. In particular, we can distinguish between habitual or exclusive bipeds and habitual or exclusive quadrupeds mainly by looking at the vertebral column between shoulders and hips. Because of the marked differences between the patterns of bending moments in bipeds and quadrupeds respectively, we usually do not need much more information than the shape of the vertebral column to distinguish between these basically different body postures. A more detailed picture of the body posture of a dinosaur, which includes, for example, the posture of the neck, can be drawn if reliable information about the distribution of body mass is available. With a more sophisticated approach, including separate analyses of lever arms of epaxial muscles and cross sections of vertebral centra, it is possible to provide a new evidence not only on the posture of a dinosaur but also on how it moved, or what it did with its head and neck.

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REFERENCES

- ALEXANDER, R. McN. 1982. *Locomotion of animals*. Blackie, Glasgow and London, vii + 163 pp.
 — 1985. Mechanics of posture and gait of some large dinosaurs. *Zoological Journal of the Linnean Society*, **83**, 1–25.
 — 1989. *Dynamics of dinosaurs and other extinct giants*. Columbia University Press, New York, 167 pp.
 — and JAYES, A. S. 1981. Estimates of the bending moments exerted by the lumbar and abdominal muscles of some mammals. *Journal of Zoology*, **194**, 291–303.

- CHRISTIAN, A. 1995. Zur Biomechanik der Lokomotion vierfüßiger Reptilien (besonders der Squamata). *Courier Forschungs-Institute Senckenberg*, **180**, 1–58.
- HORN, H.-G. and PREUSCHOFT, H. 1994a. Bipedie bei rezenten Reptilien. *Natur und Museum*, **2**, 45–57.
- ——— 1994b. Biomechanical reasons for bipedalism in reptiles. *Anphibia-Reptilia*, **15**, 275–284.
- KOBERG, D. and PREUSCHOFT, H. in press. Shape of the pelvis and posture of the hindlimbs in *Plateosaurus*. *Paläontologische Zeitschrift*.
- COOPER, M. R. 1981. The prosauropod dinosaur *Massospondylus carinatus* OWEN from Zimbabwe: its biology, mode of life and phylogenetic significance. *Occasional Papers, National Museum Monuments of Rhodesia*, **6** (B), 689–840.
- CURRIE, P. J. and SARJEANT, W. A. S. 1979. Lower Cretaceous dinosaur footprints from the Peace River Canyon, British Columbia, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **28**, 103–115.
- DODSON, P. and CURRIE, P. J. 1990. Neoceratopsia. 593–618. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. University of California Press, Berkeley, Los Angeles and London, 733 pp.
- FARLOW, J. O. and DODSON, P. 1975. The behavioral significance of frill and horn morphology in ceratopsian dinosaurs. *Evolution*, **29**, 353–361.
- GALTON, P. M. 1976. Prosauropod dinosaurs (Reptilia: Saurischia) of North America. *Postilla, Yale Peabody Museum*, **169**, 1–98.
- HEERDEN, J. van 1979. The morphology and taxonomy of *Euskelosaurus* (Reptilia: Saurischia; Late Triassic) from South Africa. *Navorsinge Nasionale Museum Bloemfontein*, **4**, 21–84.
- KUMMER, B. 1959. *Bauprinzipien des Säugerskeletes*. Thieme, Stuttgart, 279 pp.
- NORMAN, D. B. 1986. On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, **56**, 281–372.
- and WEISHAMPEL, D. B. 1990. Iguanodontidae and related Ornithopoda. 510–533. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. University of California Press, Berkeley, Los Angeles and London, 733 pp.
- PAUWELS, F. 1965. *Gesammelte Abhandlungen zur funktionellen Anatomie des Bewegungsapparates*. Springer Verlag, Berlin, Göttingen, Heidelberg, 543 pp.
- PREUSCHOFT, H. 1969. Statische Untersuchungen am Fuß der Primaten. I. Phalangen und Metatarsalia. *Zeitschrift für Anatomie und Entwicklungs-Geschichte*, **129**, 285–345.
- 1970. Statische Untersuchungen am Fuß der Primaten. II. Statik des gesamten Fußes. *Zeitschrift für Anatomie und Entwicklungs-Geschichte*, **131**, 156–192.
- 1971. Body posture and mode of locomotion in early Pleistocene hominids. *Folia Primatologica*, **14**, 209–240.
- 1976. Funktionelle Anpassung evolvierender Systeme. *Aufsätze und Reden der Senckenbergischen Naturforschenden Gesellschaft*, **28**, 98–117.
- 1989. The external forces and internal stresses in the feet of dressage and jumping horses. *Zeitschrift für Säugetierkunde*, **54**, 172–190.
- and FRITZ, M. 1977. Mechanische Beanspruchung im Bewegungsapparat von Springpferden. *Fortschritte der Zoologie*, **24**, 75–98.
- and NIEMITZ, C. 1979. The biomechanics of the trunk in primates and problems of leaping in *Tarsius*. 327–345. In MORBECK, M. E., PREUSCHOFT, H. and GOMBERG, N. (eds). *Environment, behavior and morphology: dynamic interactions in primates*. Fischer, New York, 410 pp.
- and GÜNTHER, M. M. 1994. Biomechanics and body shape in primates compared with horses. *Zeitschrift für Morphologie und Anthropologie*, **80**, 149–165.
- THULBORN, R. A. 1990. *Dinosaur tracks*. Chapman and Hall, London, New York, Tokyo, Melbourne, Madras, 410 pp.
- WEISHAMPEL, D. B. and WESTPHAL, F. 1986. *Die Plateosaurier von Trossingen*. Attempto, Tübingen, 27 pp.

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